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Research Paper

Diversity of genes for resistance to stripe rust in wheat elite lines, commercial varieties and landraces from Lebanon and Syria

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Summary. Stripe (yellow) rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a major threat to wheat production in Central and West Asia and North Africa (CWANA). Effective fungicides are available, but host resistance remains the most economical, effective and ecologically sustainable method for stripe rust control. Understanding the genetic diversity of resistance to *Pst* is a key element in breeding for durable rust resistance. Multipathotype tests were performed on 87 elite lines of bread wheat from the spring wheat breeding programme at the International Center for Agricultural Research in Dry Areas (ICARDA), 23 Lebanese bread and durum wheat varieties, and 28 Lebanese landraces, with 11 *Pst* pathotypes. Low and high infection types were identified for the resistance genes *Yr1*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr9*, *Yr17*, *Yr25*, *Yr27*, and *Yr32*. All but one of these genes (*Yr32* being the exception) were postulated. ICARDA elite lines displayed greater diversity for *Yr* genes than the Lebanese varieties and landraces. *Yr27* was the most frequent *Yr* gene postulated singly in the Lebanese varieties. *Yr7*, together with other unidentified *Yr* genes, was the most frequent gene in the ICARDA elite lines. Combinations of two *Yr* genes were common in ICARDA elite lines. These results confirm that the landraces consist of several genotypes. Seventy-five percent of landraces were susceptible to all pathotypes, but they displayed resistance diversity, with different proportions of resistant seedlings. In two landraces, some plants were resistant to the Warrior pathotype, which has recently spread in CWANA regions, and to other pathotypes. This indicates the presence of new resistance genes in these landraces. Some landraces, elite ICARDA lines and Lebanese varieties were completely resistant to all pathotypes, and are therefore potential sources of new resistances.

Keywords. Stripe (yellow) rust, wheat, gene postulation, seedling resistance.

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INTRODUCTION

In the context of global warming and the food insecurity, it is likely to cause, feeding the expanding world population through sustainable agricultural practices is a major challenge. With predicted world population of nine

billion by 2050, the demand for wheat is expected to increase by 60%. Annual increases in wheat yields will need to increase from the current level of 1% to at least 1.6% to meet this demand (Lucas, 2012).

Stripe rust, caused by the biotrophic fungus *Puccinia striiformis* f. sp. *tritici* (*Pst),* is a common wheat disease of economic importance in all world wheat production regions (de Vallavieille-Pope *et al*., 2012). In most of these areas stripe rust causes yield losses of 10-70% (Chen, 2005), depending on the time at which initial infections occur, host population density, susceptibility and nutritional status, disease development, and the duration of the epidemics. The last 40 years have seen five major stripe rust epidemics in the Central and West Asia and North Africa region (CWANA), in 1973, 1978, 1995, 2005 and 2010 (Solh *et al*., 2012). The two most recent epidemics were due to the successive emergence of *Pst* pathotypes with new virulence factors overcoming the widely used *Yr9* and *Yr27* resistance genes (Yahyaoui *et al*., 2002; Hodson and Nazari, 2010; Sharma-Poudyal *et al*., 2013). According to Hovmøller *et al*. (2011), PstS2, an aggressive strain with virulence against *Yr* genes *2*, *6*, *7, 8*, *9*, *25*, and *27,* was present at high frequency in the Red Sea area, East Africa and in Western and Central Asia between 2003 and 2008. The PstS2 strain was first detected in North America in 2000 (Milus *et al*., 2009). It was present in 50% of the virulence profiles of rust isolates surveyed in Syria in 2011 (El Amil *et al*., in press). The recent spread of Warrior pathotypes to this region (Mert *et al*., 2016) has added an additional dimension to the widespread stripe rust epidemics in wheat-growing areas in CWANA.

This damaging fungus causes losses of wheat grain yield and quality, by reducing tillering and causing grain to shrivel (Roelfs *et al.,* 1992), unless it is controlled by the use of resistant cultivars or timely fungicide applications (Hau and de Vallavieille-Pope, 2006). The deployment and use of resistant cultivars is the most economical and environmentally-friendly measure for controlling this disease (Pathan and Park, 2007). Effective deployment of resistance genes for the management of stripe rust in wheat requires knowledge of the resistance status and diversity of the resistance genes in available cultivars (Nazari *et al*., 2008). The durability of resistance may be threatened by the frequent emergence of new pathotypes. An understanding of the *Pst* population is therefore crucial in gene deployment strategies (McDonald and Linde, 2002). These strategies involve: i) the deployment of new resistance genes in a controlled manner and over a restricted geographic scale; ii) the combination of several resistance genes within a single cultivar to slow the emergence of new virulent pathotypes; and iii) the combination of race-specific resistance with non race-specific or partial resistance within a single cultivar. These approaches require a knowledge of the resistance genes present in the breeding germplasm and commercial cultivars. It is, therefore, important to identify the resistance genes present in different cultivars, because cultivars may have resistance genes in common, even if they originated from genetically different sources. Knowledge of the resistance genes present makes it possible to prevent the release of mega-cultivars containing the same resistance genes or profiles (Statler, 1984).

Gene postulation is based on the theory of a gene-for-gene relationship (Flor, 1956), according to which it is possible to postulate the existence of race-specific genes for resistance in a cultivar provided with an array of pathotypes bearing diverse combinations of avirulence and virulence genes. This approach can be used for the rapid identification of probable race-specific rust resistance genes (*Yr*) in a large group of wheat lines. This method has traditionally been used for the three rust diseases (Perwaiz and Johnson, 1986; Nazari *et al*., 2008). Stripe rust resistance genes have been postulated in wild emmer wheat derivatives and advanced wheat lines from Nepal (Sharma *et al*., 1995), French wheat lines (de Vallavieille-Pope *et al*., 1990; Robert *et al*., 2000), Danish wheat cultivars (Hovmøller, 2007), Chinese wheat cultivars and advanced lines (Xia *et al*., 2007), and Ethiopian bread wheat cultivars (Dawit *et al*., 2012).

Landraces of cultivated plants were the principal focus of agricultural production until the end of the nineteenth century and the advent of formal plant breeding (Harlan, 1975). According to Camacho Villa *et al*. (2005), "a landrace is a dynamic population of a cultivated plant that has a historical origin, distinct identity and lacks formal crop improvement, as well as often being genetically diverse, locally adapted and associated with traditional farming systems". Modern cereal cultivars are derived from narrow germplasm pools and are mostly adapted to high-input agriculture. A distinction is made between landraces and the modern, so-called "elite" lines generated by formal crop breeding programmes (Newton *et al*., 2010). Landraces may be good reservoirs of non race-specific or partial resistances capable of conferring durability when combined with major resistance genes commonly exploited in modern cultivars. Given that landraces are adapted to local edaphic and climatic conditions and display tolerance or resistance to many pests and diseases, their use could expand the narrow genetic basis of elite lines (Beharav *et al*., 1997). Zhang (1995) showed that nine Chinese wheat landraces expressed slow rusting or quantitative

resistance to stripe rust. Lebanon is located in the Fertile Crescent, the area in which wheat and its wild relatives are most diverse (Harlan and Zohary, 1966). Lebanese landraces are, therefore, also likely to be promising sources of novel resistance genes with major and partial effects. The identification of seedling rust resistance genes in Lebanese landraces is, therefore, an important first step towards further wheat improvement in the CWANA region.

The genes conferring resistance to wheat stripe rust in ICARDA elite breeding lines, Lebanese cultivars and Lebanese landraces, remain largely unknown. The present study aimed to provide detailed information about specific resistance to wheat stripe rust, detectable at the seedling stage, in 87 elite lines of bread wheat from the spring wheat breeding programme at ICARDA, 23 Lebanese bread and durum wheat varieties and 28 Lebanese landraces. Gene postulation was performed with an array of 11 *Pst* pathotypes that distinguished between low and high infection types for the resistance genes *Yr1*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr17*, *Yr25*, *Yr27*, *Yr32*, *YrSD*, *YrSu* and *YrSP*. Adult plant resistance was also evaluated in some ICARDA lines.

MATERIALS AND METHODS

Pathogen material

The virulence combinations and pathotype codes of the *Pst* isolates used for resistance gene postulation were determined with the European and World sets of 15 differential varieties (Johnson *et al*., 1972), 13 Avocet lines near-isogenic for *Yr1*, *Yr5*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr15*, *Yr24*, *Yr26*, *Yr27*, *Yr32* and *YrSP* (Wellings *et al*., 2009), and the lines Kalyansona (*Yr2*), Federation 4*/ Kavkaz (*Yr9*), Clement (*Yr9+*), VPM1 (*Yr17+*), TP981 (*Yr25*) and Opata (*Yr27*). Each differential line carries at least one race-specific resistance gene (*Yr*) expressed at the seedling growth stage.

Resistance genes were postulated at the seedling stage at the INRA BIOGER rust facility, on the basis of infection types (IT), with a set of 11 French pathotypes displaying complementary virulences, including the recently propagated Warrior race (Table 1) (de Vallavieille-Pope *et al*., 2012). As most of these pathotypes present more than one avirulence factor, it was not always possible to infer precise resistance gene combinations.

All isolates from the INRA-Grignon collection were purified from single spores, and were stored in liquid nitrogen. Spore multiplication was performed in a controlled climate chamber. Reference isolate spores were used to inoculate 7-d-old seedlings of the susceptible cultivar 'Victo', which was then incubated in a dew chamber at 8°C for 16 h in the dark to ensure successful infection, before transfer to a controlled climate chamber (day: 16 h, 300 μmol m^{-2} s^{-1}, 17°C; night: 8 h, 14°C). Seedlings were exposed to high-intensity light treatment at 200 μE m^{-2} s^{-1} for at least 8 h before inoculation, to maximize infection efficiency (de Vallavieille-Pope *et al*., 2002). One week after inoculation, each pot was sealed in a cellophane bag to prevent cross-contamination. Uredospores were collected 18 d post-inoculation, were

Table 1. Pathotype code, name and avirulence/virulence formula of 11 French *Puccinia striiformis* f. sp. *tritici* pathotypes used for the postulation of stripe rust resistance genes in Syrian and Lebanese wheat genotypes.

Pathotype code	Pathotype nomenclature[a]	Avirulence formula[b]	Virulence formula
A	6E16	*1, 3, 4, 5, 9, 10, 15, 17, 24, 25, 26, 27, 32, SD, Su, ND, SP*	*2, 6, 7, 8*
B	6E16*v9v27*	*1, 3, 4, 5, 10, 15, 17, 24, 26, 32, SD, Su, ND, SP*	*2, 6, 7, 8, 9, 25, 27*
C	43E138	*4, 5, 6, 8, 9, 10, 15, 17, 24, 26, 27, 32, Su, SP*	*1, 2, 3, 7, 25, SD, ND*
D	45E140	*4, 5, 7, 8, 9, 10, 15, 17, 24, 26, 27, 32, Su, SP*	*1, 2, 3, 6, 25, SD, ND*
E	106E139	*1, 5, 6, 8, 9, 10, 15, 17, 24, 26, 27, 32, SP*	*2, 3, 4, 7, 25, SD, Su, ND*
F	169E136*v17*	*4, 5, 6, 7, 8, 10, 15, 24, 26, 27, 32, Su, SP*	*1, 2, 3, 9, 17, 25, SD, ND*
G	232E139	*1, 5, 6, 7, 8, 10, 15, 17, 24, 26, 27, 32, SP*	*2, 3, 4, 9, 25, SD, Su, ND*
H	237E140	*5, 7, 8, 10, 15, 17, 24, 26, 27, 32, SP*	*1, 2, 3, 4, 6, 9, 25, SD, Su, ND*
I	237E141*v17*	*5, 7, 8, 10, 15, 24, 26, 27, 32, SP*	*1, 2, 3, 4, 6, 9, 17, 25, SD, Su, ND*
J	237E173*v17 (Oakley/Solstice)*	*5, 7, 8, 10, 15, 24, 26, 27, SP*	*1, 2, 3, 4, 6, 9, 17, 25, 32, SD, Su, ND*
K	239E175*v17 (Warrior)*	*5, 8, 10, 15, 24, 26, 27*	*1, 2, 3, 4, 6, 7, 9, 17, 25, 32, SD, Su, ND, (SP)*[c]

[a] Pathotype nomenclature is based on Johnson *et al*. (1972).
[b] *YrSD*, *YrSu*, *YrND* and *YrSP*, correspond to, respectively, Strubes Dickkopf, Suwon 92 × Omar, Nord Desprez and Spaldings Prolific.
[c] *SP* infection types 5 to 6 were considered to be intermediate reactions, and are shown in parentheses.

dried in a desiccator containing silica gel at 4°C for 3 d, and were then stored in liquid nitrogen (LN). Any cold dormancy of samples stored in LN was broken by subjecting the uredospores to a heat shock (40°C for 10 min) before inoculation in *Yr*-gene postulation tests.

Host material

We tested 138 genotypes at the seedling stage. These included: 87 advanced lines of bread wheat from the spring wheat breeding programme at ICARDA (Table S1), 23 cultivars commonly grown in Lebanon (13 of bread wheat and ten of durum wheat) (Table S2), and 28 Lebanese landraces (21 accessions of bread wheat and seven of durum wheat; Table S2). Seed stocks for elite lines and landraces were obtained, respectively, from ICARDA and the Lebanese Agriculture Research Institute (LARI). Landraces are known to be highly diverse and heterogeneous. Landrace seeds were therefore collected from a number of different sites in Lebanon, to obtain a broad genetic pool. The seeds were then purified at LARI for morphological traits corresponding to the criteria for use in agriculture, before the resistance gene tests (Table 2).

Inoculation and scoring

All seeds were planted in square pots (7 × 7 × 8 cm) filled with standard peat soil. Five seeds of each elite line and variety and 15 seeds of each landrace were planted in two replicated pots. The pots were placed in air-filtered cabinets in a glasshouse, at temperatures between 15 and 25°C, with a 16-h photoperiod extended with sodium vapour lamps, for 10 d. The seedlings were inoculated with spores when they were 2 weeks old and with second leaves fully expanded. The inoculated spores had been stored at –80°C, then taken out of the freezer and immediately heat shocked at 40°C for 10 min before use. Spores (3 mg) were suspended in 600 µL of engineered fluid (NovecTM 7100) for inoculation onto seedlings. Inoculated plants were incubated for 24 h in the dark in a dew chamber at 8°C and 100% relative humidity, after which they were placed in cabinets with the conditions described above. The experiment was performed twice.

Seedling infection types were recorded 15–17 d after inoculation, using a 0–9 scale based on the presence of necrosis, chlorosis, size of sporulation areas and sporulation intensity (McNeal *et al*., 1971). Infection types (IT) 0 to 4 were considered to indicate various levels of incompatibility (host resistance and pathogen avirulence) between host and pathogen, whereas infection types 7 to 9 were considered to correspond to compatible (host susceptibility and pathogen virulence) interactions. Infection types 5 to 6 were considered to be intermediate reactions (Roelfs *et al.,* 1992). Resistance genes were postulated by comparing the low and high IT patterns obtained with the pathotype array on the tested entities with those of differential lines with known resistance genes. If a wheat variety had a low/high IT pattern similar to that of a differential line with a known resistance profile, the tested genotype was postulated to possess the same resistance genes as the differential. This method was applied successively to all *Yr* genes detectable with the array of 11 pathotypes used for the study.

The diversity of seedling resistance within the Lebanese wheat landrace collections was investigated by assessing the frequency of resistant plants in the overall susceptible landrace population and the frequency of susceptible plants in the overall resistant landrace population, for the 11 *Pst* pathotypes (Table 6).

Assessment of adult plant resistance

The ICARDA elite lines tested at the seedling stage against pathotype 6E16*v9v27* (the most prevalent *Pst* pathotype in Syria and Lebanon during the 2010–2011 cropping season) included 44 lines containing postulated resistance gene and/or gene combinations that were assessed for adult-plant resistance. The experiments on adult plants were performed with this pathotype at the ICARDA research stations in Tal Hadya, Syria in 2009-2011, and Terbol, Lebanon in 2009–2013 (Table 5).

At each site, 30 seeds of each genotype were planted in two 0.5 m rows in a field nursery in November in each year. The highly susceptible 'Morocco' and two cultivars known to carry *Yr9* (Seri-82) and *Yr27* (Cham-8) were planted as spreader rows bordering the trial areas, in all pathways, and at ten-row intervals within the trial. The inoculum used for this study comprised the dominant pathotypes collected separately in Syria or Lebanon from natural infections in the same fields during the previous year. The inoculated pathotypes carried virulence against the genes *Yr2*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr25*, *Yr27* and *YrSD*. The trail fields were dusted in the evenings with a spore-talc mixtures (1 to 50), at the seedling, tillering, and flag leaf stages. Disease infection types were recorded as described by Roelfs *et al*. (1992), and the modified Cobb scale was used to assess disease severity (Peterson *et al*., 1948) at the host booting and flag leaf stages. Flag leaf scoring was used to assess the final disease responses of the tested genotypes at the adult plant growth stage.

Table 2. Resistance group, seedling infection types and postulated stripe rust resistance genes in 87 wheat elite lines from ICARDA, tested against 11 *Puccinia striiformis* f. sp. *tritici* pathotypes.

Group	Entry No.	Genotype	Pathotype code [a]											Postulated *Yr* genes
			A	B	C	D	E	F	G	H	I	J	K	
1	**3**	Tabeldi-1	1	1	3	6	1	5	1	3	2	2	5	Resistant[b]
	11	Babaga-3	1	2	3	6	1	5	1	3	2	2	4	Resistant
	20	Sale-6	1	1	2	2	1	2	1	2	2	2	3	Resistant
	32	Hashab-2	1	1	2	2	1	4	1	2	2	2	4	Resistant
	40	Usher-18	1	5	4	3	3	3	2	2	2	3	4	Resistant
	45	Saba/Flag-1	2	6	2	2	2	2	2	2	2	2	4	Resistant
	72	Naji-3	1	2	3	4	1	6	1	2	2	2	5	Resistant
	78	Shuha-8/Ducula	1	1	2	2	1	3	1	2	2	2	4	Resistant
2	**12**	Cham-6	8	7	8	8	9	8	8	8	8	8	8	Susceptible[c]
	75	Nesma*2/14-2//2*Safi-3	8	7	8	8	9	8	8	8	8	8	8	Susceptible
	79	Shuha-8/Ducula	8	6	8	8	8	8	8	8	8	6	8	Susceptible
3	6	Utique 96/Flag-1	4	7	3	8	9	5	9	8	8	8	8	Ni[d]
	7	Hamam-4	1	7	1	1	1	5	7	3	8	8	4	Ni
	16	Durra-8	2	8	3	6	9	5	8	3	8	8	2	Ni
	22	Fow-2/SD8036//SafiI-3/3/NS732/HER//Kauz'S'	3	8	5	8	8	8	8	3	8	5	2	Ni
	30	Sandall-5	2	3	2	2	2	9	2	2	8	8	8	Ni
	38	Temerind-8	1	8	1	8	-[e]	2	3	2	2	2	4	Ni
	39	Gonglase-4	2	2	8	1	2	9	2	8	8	8	8	Ni
	48	Bushraa-3	5	3	3	2	4	8	2	4	3	2	8	Ni
	54	Jasmin-5	2	2	3	7	8	8	8	8	4	3	3	Ni
	57	Qadanfer-5	7	8	4	3	8	5	8	6	2	3	8	Ni
	62	Tevee'S'/3/T.aestivum/SPRW'S'//CA8055/4/Pastor-2/5/Sunbri	1	1	8	8	1	8	1	8	4	8	8	Ni
	69	Manhal-4	2	2	8	8	1	1	6	6	2	8	8	Ni
	21	HD2206/Hork'S'/3/2*NS732/HER//Kauz'S'	4	6	5	8	7	9	8	7	7	8	8	Ni
	85	Girwill-13/2*Pastor-2	1	8	3	2	2	4	8	8	8	8	8	Ni
	14	Jawahir-14	6	1	8	8	1	9	1	8	8	8	8	Ni
		Chinese 166[f]	1	1	9	9	1	8	1	9	9	9	9	*Yr1*
4		**Avocet *Yr1*/6*Avocet S**	2	1	8	8	2	8	1	8	8	8	9	*Yr1*
	60	Crow'S'/Bow'S' -3-1994/95//Tevee'S'/Tadinia	1	1	8	8	1	9	1	8	7	8	7	*Yr1*
	61	Tevee'S'/3/T.aestivum/SPRW'S'//CA8055/4/Pastor-2/5/Sunbri	1	1	8	8	1	9	1	8	8	8	8	*Yr1*
	65	Qafzah-2/Ferroug-2	1	2	8	8	1	9	2	8	8	8	8	*Yr1*
	70	Usher-16	1	2	8	8	1	8	1	8	8	8	8	*Yr1*
	74	Settat-45	2	2	8	8	1	7	1	8	8	8	8	*Yr1*
		Vilmorin 23	2	3	8	8	9	8	8	9	9	9	9	*Yr3*
5	**46**	Bow #1/Fengkang15/3/HYS//DRC*2/7C	5	3	8	8	8	9	7	8	8	8	8	*Yr3*
6		**Hybrid 46**	2	1	1	2	9	2	8	9	9	9	8	*Yr4*
	33	Sanobar-1	2	3	2	2	8	2	8	8	8	8	8	*Yr4*
	18	Sanobar-6	2	2	2	2	8	2	8	6-7	8	8	8	*Yr4*
	82	ESWYT99#18/Arrihane	2	5	4	2	8	3	7	8	8	8	8	*Yr4*
7		**Avocet *Yr6*/6*Avocet S**	8	8	3	8	4	4	4	8	8	8	8	*Yr6*
		Heines Kolben	9	9	2	9	2	2	1	9	9	9	9	*Yr6, Yr2*
	67	Hamam-4/Angi-2	8	8	3	8	3	3	2	8	8	8	8	*Yr6*
	87	Hubara-16/2*Somama-3	7	8	2	8	2	2	3	8	6	8	8	*Yr6*
		Heines Peko	2	4	2	9	2	2	2	9	9	9	8	*Yr6, Yr+*
	2	Zafir-3	2	2	2	9	2	2	2	2	2	7	8	*Yr6, Yr+*

(Continued)

Table 2. (Continued).

Group	Entry No.	Genotype	Pathotype code [a]											Postulated *Yr* genes
			A	B	C	D	E	F	G	H	I	J	K	
	5	Aguilal/Flag-3	2	3	2	8	2	2	2	8	5	8	8	*Yr6, Yr+*
	47	Faisal-1	1	5	4	8	1	3	4	7	8	8	8	*Yr6, Yr+*
	63	Weebill-1/2*Qafzah-21	4	6	3	7	7	2	5	8	8	8	8	*Yr6, Yr+*
	64	Rebwah-12/Zemamra-8	2	1	2	2	1	3	1	8	8	8	8	*Yr6, Yr+*
8		**Avocet *Yr7*/6*Avocet S**	8	8	8	3	8	4	4	2	3	3	8	*Yr7*
		Lee	9	9	9	3	9	3	2	3	3	3	9	*Yr7, Yr+*
		Reichersberg 42	2	4	9	2	9	2	2	2	2	2	8	*Yr7, Yr+*
	43	Soonot-11	1	2	1	1	1	1	2	2	2	2	8	*Yr7, Yr+*
	23	Neem-2	1	2	1	1	1	1	2	2	2	2	8	*Yr7, Yr+*
	34	Cham-10	1	1	1	1	1	1	2	1	2	2	8	*Yr7, Yr+*
	19	Reyna-12	1	1	1	1	1	1	2	1	2	2	8	*Yr7, Yr+*
	36	Reyna-25	1	1	1	1	-	1	2	1	2	2	8	*Yr7, Yr+*
	41	Florkwa-2/Asfoor-5	1	2	1	1	1	1	2	2	2	2	8	*Yr7, Yr+*
	42	Settat-13	1	2	1	1	1	1	3	2	2	2	8	*Yr7, Yr+*
	44	Hubara-15/Zemamra-8	1	1	1	1	1	3	1	2	3	5	8	*Yr7, Yr+*
	37	Reyna-29	1	2	1	1	1	1	2	2	2	2	8	*Yr7, Yr+*
	68	Sisaban-3	1	1	1	1	1	1	2	1	2	2	8	*Yr7, Yr+*
	77	Achta*3//Kanz/KS85-8-4/3/Lakta-8/4/Zemamra-1	2	2	2	1	2	1	2	2	2	2	8	*Yr7, Yr+*
	52	Reyna-24	1	1	1	1	1	1	1	1	1	1	8	*Yr7, Yr+*
	17	Laloub-2	1	1	1	1	1	1	2	1	2	2	8	*Yr7, Yr+*
	81	Achtar/INRA 1764	2	8	2	5	2	3	2	2	4	6	8	*Yr7, Yr+*
	80	Achtar/INRA 1764	2	8	3	3	2	4	3	4	3	6	8	*Yr7, Yr+*
9		**Avocet *Yr9*/6*Avocet S**	2	8	2	2	2	8	8	8	8	8	8	*Yr9*
		Clement	1	5-6	2	1	2	8	8	8	8	8	9	*Yr9*
		Federation 4*/ Kavkaz	1	9	2	1	1	8	8	9	9	9	9	*Yr9*
	66	Haala-50	3	8	5	1	1	8	8	7	8	8	8	*Yr9*
	28	Battell-3	2	8	2	2	2	8	9	-	8	8	8	*Yr9*
	29	Sandall-3	1	8	2	2	2	8	9	-	8	8	8	*Yr9*
	35	ICARDA-SRRL-5	2	8	2	2	2	8	8	-	8	8	8	*Yr9*
10		**VPM1**	2	3	2	2	2	8	2	2	9	9	9	*Yr17*
	13	Ruth-1	1	1	1	2	1	7	1	2	8	8	8	*Yr17*
	49	Nouha-3	1	4	2	2	1	8	2	2	8	8	8	*Yr17*
	31	Samira-2	1	2	5	2	1	5	2	3	8	8	8	*Yr17+*
11		**TP981**	2	8	9	9	9	8	8	9	9	9	9	*Yr25*
	15	Nayzak-3	1	8	8	9	9	9	8	8	8	8	8	*Yr25*
12		**Avocet *Yr27*/6*Avocet S**	5	8	3	2	3	3	2	3	2	2	3	*Yr27*
		Opata	5	8	3	2	3	3	2	3	2	2	3	*Yr27*
	1	Cham-8	1	8	1	1	1	2	2	2	2	2	5	*Yr27*
	8	Inqualab 91/Flag-2	4	8	2	3	2	2	2	2	3	3	4	*Yr27*
	10	Bow#1/Fengkang15/3/HYS//DRC*2/7C	2	8	2	3	2	2	2	2	2	2	2	*Yr27*
	53	NS732/HER//SD8036/3/Saada	2	7	2	2	2	2	5	2	2	2	2	*Yr27*
	56	Loulou-16	1	8	1	1	1	2	2	2	2	2	3	*Yr27*
	73	HIJLEEJ-1	2	8	4	2	5	3	2	2	2	2	3	*Yr27*
	76	NS732/HER*2//Saada	2	8	2	2	3	2	2	2	2	2	2	*Yr27*
	58	Taleh-1	1	8	1	1	1	2	4	2	2	3	4	*Yr27*

(Continued)

Table 2. (Continued).

Group	Entry No.	Genotype	Pathotype code [a]										Postulated *Yr* genes
			A	B	C	D	E	F	G	H	I	J	K	
13	**51**	Sidraa-1	4	6-7	3	4	5	2	5	8	8	8	8	*Yr6 + Yr9*
	71	Latifa-2	1	8	1	1	1	5	4	8	8	8	8	*Yr6 + Yr9*
	27	Koukab-2	1	3	2	1	1	4	4	2	8	7	8	*Yr6 + Yr17*
	86	Hubara-3/Angi-2//Somama-3	1	1	2	1	1	2	1	4	7	8	8	*Yr6 + Yr17*
	24	Firdous-29	2	1	7	3	2	2	1	2	3	2	8	*Yr7 + Yr1*
	26	Saamid-2	2	2	2	1	7	1	2	2	2	2	8	*Yr7 + Yr4*
	4	Soonot-10	2	2	1	1	9	1	2	2	2	2	8	*Yr7 + Yr4*
	59	Nadia-13	2	2	2	1	8	2	2	2	2	2	8	*Yr7 + Yr4*
	84	ACSAD 529/Karawan'S'//Somama-3	1	1	3	2	1	9	1	8	8	8	8	*Yr9 + Yr1*
	83	Hubara-5/3/SHA3/Seri//SHA4/Lira	1	2	2	3	2	8	8	9	8	8	8	*Yr9 + Yr3*
	9	Qafzah-33/Florkwa-2	1	4	2	2	1	3	8	-	8	8	8	*Yr9 + Yr4*
	25	Jelmoud-1	1	1	1	1	2	1	8	-	8	8	8	*Yr9 + Yr4*
	50	Milan/SHA7//Potam*3KS811261-5	1	4	1	1	2	3	8	-	7	8	8	*Yr9 + Yr4*
	55	Fanoos-14	1	2	1	1	1	3	8	-	8	8	8	*Yr9 + Yr4*

[a]A = 6E16, B = 6E16*v9v27*, C = 43E138, D = 45E140, E = 106E139, F = 169E136*v17*, G = 232E137, H = 237E141, I = 237E141*v17*, J = 237E173*v17 (Oakley/Solstice)*, K = 239E175*v17 (Warrior)*. Pathotypes are coded according to Johnson *et al.* (1972).
The virulences and avirulences tested were 1, 2, 3, 4, 6, 7, 8, 9, 17, 25, 27, 32, SD, SP, Su. Scoring was performed as described by McNeal *et al.* (1971); Infection types IT0 = No visible uredia, IT1 = Necrotic flecks, IT2 = Necrotic areas without sporulation, IT3-4 = Necrotic and chlorotic areas with restricted sporulation, IT5-6 = Moderate sporulation with necrosis and chlorosis, IT7-8 = Sporulation with chlorosis, IT9 = Abundant sporulation without chlorosis.
[b] Resistant to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.
[c] Susceptible to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.
[d] Ni indicates non-identified resistance genes.
[e] Indicates missing data.
[f] The entries in bold font correspond to the infection type profiles of the tester lines confronted with the array of 11 *Puccinia striiformis* f. sp. *tritici* pathotypes.

Statistical analyses

Principal component analysis (PCA) was performed to illustrate the heterogeneity of the distributions of resistant and susceptible plants for each pathotype tested on landraces. The heterogeneity of resistance in landraces was assessed by determining the percentage of resistant plants in landraces mostly susceptible to one pathotype and the percentage of susceptible plants in landraces mostly resistant to one pathotype. Data were plotted for 11 variables, corresponding to the 11 pathotypes tested. Another PCA was performed on the percentage of plants in each landrace resistant to each of the 11 pathotypes. PCAs were performed with R software (http://www.R-project.org, 2008).

RESULTS

Postulation of seedling resistance genes

The seedling tests conducted on the 138 elite lines, varieties and landraces with 11 French *Pst* pathotypes made it possible to postulate genes for seedling resistance to stripe rust, either singly or in combinations (Tables 2, 3, and 4; Figure 1). The pathotypes used made postulation possible for *Yr1*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr9, Yr17, Yr25*, *Yr27* and *Yr32*. Based on these postulations, the lines were attributed to 13 stripe rust resistance groups.

Tested lines resistant to all 11 pathotypes were classified into group 1, those susceptible to all 11 pathotypes were classified into group 2, and tested lines that could not be characterized with the set of 11 pathotypes were classified into group 3.

Resistance group 1 corresponded to genotypes resistant to all *Pst* pathotypes. This group included eight ICARDA elite lines of bread wheat (Table 2) and two Lebanese durum wheat varieties (Table 3). These genotypes had low to intermediate ITs for all pathotypes tested. They therefore possessed a *Yr* gene or combination of *Yr* genes without corresponding virulence in the 11 *Pst* pathotypes.

Resistance group 2 corresponded to the genotypes susceptible to all *Pst* pathotypes, which therefore harboured no *Yr* genes, although they may have harboured

Table 3. Resistance group, infection type and postulated seedling-stage stripe rust resistance genes against 11 *Puccinia striiformis* f. sp. *tritici* pathotypes, for 23 Lebanese wheat varieties.

Resistance group	Wheat line	Pathotype code[a]											Postulated *Yr* genes
		A	B	C	D	E	F	G	H	I	J	K	
1	Stork	1	3	2	2	3	4	4	2	2	2	1	Resistant[b]
	Azeghar	3	3	2	2	2	1	2	2	2	2	2	Resistant
2	Super X	8	8	8	8	-[c]	9	-	9	8	8	9	Susceptible[d]
3	Senatore Cappelli	4	4	2	3	8	3	7	3	2	2	1	Ni[e]
	Miki	5	5	4	8	8	5	8	5	3	3	8	Ni
	Tal Amara 2	3	2	3	8	8	5	8	8	8	8	8	Ni
	Icarasha	4	4	2	8	2	2	2	2	4	2	8	Ni
	Tal Amara 1	4	3	1	8	2	2	1	4	2	2	2-4	Ni
	Tal Amara 3	6	5	2	6	2	2	2	4	4	4	8	Ni
	Nab El Jamal	1	8	2	3	2	8	9	9	8	8	8	Ni
5	**Vilmorin 23** [f]	2	3	8	8	9	8	8	9	9	9	9	
	Genessi	3	3	7	8	6-7	9	8	8	8	8	8	*Yr3*
8	**Avocet *Yr*7/6*Avocet S**	8	8	8	3	8	4	4	2	3	3	8	*Yr7*
	Lee	9	9	9	3	9	3	2	3	3	3	9	*Yr7, Yr+*
	Reichersberg 42	2	4	9	2	9	2	2	2	2	2	8	*Yr7, Yr+*
	Haramoun	8	8	8	3	9	3	3	2	2	3	9	*Yr7*
	Tannour	1	8	2	1	2	2	2	2	2	2	8	*Yr7, Yr+*
	885	2	8	2	2	1	2	3	2	2	2	8	*Yr7, Yr+*
11	**TP981**	2	8	9	9	9	8	8	9	9	9	9	
	Florence Aurore	1	8	8	8	9	9	9	9	8	8	8	*Yr25*
12	**Avocet *Yr*27/6*Avocet S**	5	8	3	2	3	3	2	3	2	2	3	*Yr27*
	Opata	5	8	3	2	3	3	2	3	2	2	3	*Yr27*
	MR 1009	3	8	2-3	2	2	3	2	2	2	2	5	*Yr27*
	Katilla	1	8	1	1	1	2	2	2	2	2	2	*Yr27*
	Bouhouth 6	3	8	3	2	3	2	2	2	2	2	4	*Yr27*
	Aammoun	1	8	1	1	1	2	3	2	2	2	5	*Yr27*
	Sham 8	2	8	2	1	2	2	2	3	2	2	5	*Yr27*
13	Lahn	8	7	1	5	2	1	2	6	3	4	8	*Yr6 + Yr7*
	A1103	8	8	3	2	2	3	2	3	2	2	7	*Yr6 + Yr7*
	Naama	1	4	2	2	2	2	2	5	8	8	8	*Yr6 + Yr17*

[a]A = 6E16, B = 6E16*v9v27*, C = 43E138, D = 45E140, E = 106E139, F = 169E136*v17*, G = 232E137, H = 237E141, I = 237E141*v17*, J = 237E173*v17 (Oakley/Solstice)*, K = 239E175*v17 (Warrior)*. Pathotypes are coded according to Johnson *et al.* (1972).
The virulences and avirulences tested were 1, 2, 3, 4, 6, 7, 8, 9, 17, 25, 27, 32, SD, SP, Su. Scoring was performed as described by McNeal *et al.* (1971); Infection types IT0 = No visible uredia, IT1 = Necrotic flecks, IT2 = Necrotic areas without sporulation, IT3-4 = Necrotic and chlorotic areas with restricted sporulation, IT5-6 = Moderate sporulation with necrosis and chlorosis, IT7-8 = Sporulation with chlorosis, IT9 = Abundant sporulation without chlorosis.
[b] Resistant to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.
[c] - indicates missing data.
[d] Susceptible to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.
[e] Ni indicates non-identified resistance genes.
[f] The entries in bold correspond to the infection type profiles of the tester lines confronted with the array of 11 *Puccinia striiformis* f. sp. *tritici* pathotypes.

resistance genes corresponding to the virulence profiles of the 11 tester pathotypes resulting in compatible reactions. This group included three elite lines (Table 2), one Lebanese variety (Table 3) and 21 Lebanese landraces (Table 4; 14 populations of Salamouni wheat, three populations of Abou Shwereb wheat, two populations of Ukranian wheat, and one population each of Bekaii and Haurani wheat).

Table 4. Resistance group, infection type and postulated seedling-stage stripe rust resistance genes against 11 *Puccinia striiformis* f. sp. *tritici* pathotypes, for 28 Lebanese wheat landraces.

Resistance group	Wheat landrace	Pathotype code[a]											Postulated *Yr* genes
		A	B	C	D	E	F	G	H	I	J	K	
1	Waha	1	2	2	2	2	1	1	2	1	2	1	Resistant[b]
2	Abou Shwereb	8	8	8	7	9	9	9	9	8	8	8	Susceptible[c]
	Abou Shwereb	8	8	8	8	9	9	9	9	8	8	9	Susceptible
	Salamouni	8	8	8	8	9	9	9	9	8	8	9	Susceptible
	Salamouni	8	8	8	9	9	8	9	8	8	8	9	Susceptible
	Salamouni	8	8	8	8	9	8	9	8	8	8	8	Susceptible
	Salamouni	8	8	8	8	9	8	9	9	8	8	8	Susceptible
	Salamouni	9	8	8	8	9	8	9	9	8	8	8	Susceptible
	Ukranian	8	8	8	8	9	8	9	9	8	8	9	Susceptible
	Ukranian	8	8	8	8	9	8	9	7	8	8	8	Susceptible
	Salamouni	9	8	8	9	9	9	9	9	7	8	9	Susceptible
	Salamouni	8	8	8	9	9	8	9	9	8	8	8	Susceptible
	Abou Shwereb	9	8	8	9	9	9	9	9	8	8	9	Susceptible
	Salamouni	9	8	8	9	9	9	9	9	8	8	9	Susceptible
	Haurani	8	6-7	8	9	9	9	9	9	8	8	9	Susceptible
	Bekaii	7	8	6-7	7	9	8	9	8	8	8	9	Susceptible
	Salamouni	9	8	8	9	9	8	9	9	8	8	8	Susceptible
	Salamouni	8	8	8	9	9	8	9	9	8	8	8	Susceptible
	Salamouni	8	8	8	8	9	9	9	9	8	8	9	Susceptible
	Salamouni	8	8	8	8	9	9	9	9	8	8	9	Susceptible
	Salamouni	9	8	8	8	9	9	9	9	8	8	9	Susceptible
	Salamouni	8	8	8	8	9	9	9	9	8	8	9	Susceptible
3	Bekaii	8	8	4	8	9	9	9	8	4	3	6	Ni[e]
	Abou Shwereb	3	4	8	8	9	9	9	9	8	8	8	Ni
5	**Vilmorin 23[d]**	2	3	8	8	9	8	8	9	9	9	9	
	Awnless variety	1	3	8	8	9	9	8	9	7	7	8	*Yr3*
6	**Hybrid 46**	2	1	1	2	9	2	8	9	9	9	8	
	Nessr	2	4	2	5	9	5	9	9	8	8	8	*Yr4*
11	**TP981**	2	8	9	9	9	8	8	9	9	9	9	
	Salamouni	1	8	8	8	9	9	9	9	8	8	9	*Yr25*
	Salamouni	1	8	8	8	9	9	9	9	8	8	9	*Yr25*

[a]A = 6E16, B = 6E16*v9v27*, C = 43E138, D = 45E140, E = 106E139, F = 169E136*v17*, G = 232E137, H = 237E141, I = 237E141*v17*, J = 237E173*v17 (Oakley/Solstice)*, K =239E175*v17 (Warrior)*. Pathotypes are coded according to Johnson *et al*. (1972).
The virulences and avirulences tested were 1, 2, 3, 4, 6, 7, 8, 9, 17, 25, 27, 32, SD, SP, Su. Scoring was performed as described by McNeal *et al.*(1971); Infection types IT0 = No visible uredia, IT1 = Necrotic flecks, IT2 = Necrotic areas without sporulation, IT3-4 = Necrotic and chlorotic areas with restricted sporulation, IT5-6 = Moderate sporulation with necrosis and chlorosis, IT7-8 = Sporulation with chlorosis, IT9 = Abundant sporulation without chlorosis.
[b] Resistant to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.
[c] Susceptible to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.
[d] The entries in bold correspond to the infection type profiles of the tester lines inoculated with the array of 11 *Puccinia striiformis* f. sp. *tritici* pathotypes.
[e] Ni indicates non-identified resistance genes.

Resistance group 3 included 15 ICARDA elite lines (Table 2), one bread and six durum wheat varieties from Lebanon (Table 3), and two Lebanese durum wheat landraces that did not display clear differential responses to the 11 pathotypes used in this study. The genotypes in this group, therefore, could not be used for gene postulation (Table 4).

The tested genotypes in resistance group 4 had high ITs (7 to 9) for the seven *Pst* pathotypes virulent against

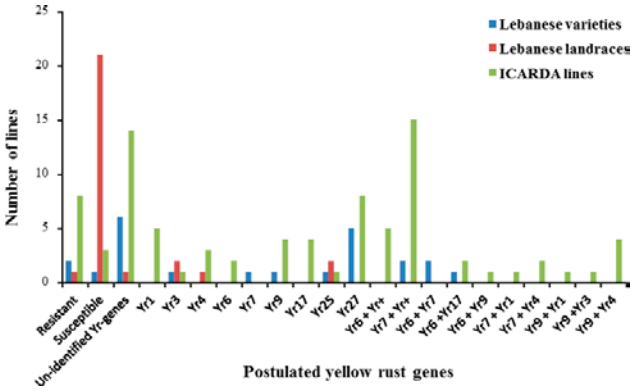

Figure 1. Postulated *Yr* seedling-stage stripe rust resistance in Lebanese wheat varieties, Lebanese wheat landraces and ICARDA wheat lines.

Yr1, and low ITs (1 to 3) for the four pathotypes avirulent against *Yr1*. This led us to postulate the presence of *Yr1* in the five ICARDA elite lines, with resistance profiles similar to those of the tester genotypes Chinese 166 and Avocet *Yr1* (Table 2). This is the first postulation of *Yr1* in Lebanese varieties and landraces.

Genotypes in resistance group 5 had high ITs (7 to 9) for the nine pathotypes virulent against *Yr3*, and low ITs (1 to 4) for pathotypes avirulent against *Yr3*. One ICARDA elite line, one Lebanese variety (Genessi), and one Lebanese bread wheat landrace (awnless variety) were postulated to have *Yr3*. These postulated lines had resistance profiles similar to that of the tester genotype Vilmorin 23 (Tables 2, 3 and 4).

Three elite lines and the bread wheat landrace Nessr were postulated to carry the *Yr4* gene (resistance group 6). The postulated lines had resistance profiles similar to that of the tester genotype Hybrid 46 (Table 1). The low to intermediate ITs (2 to 4, except for one line, ESWYT99#18/Arrihane, which had an IT of 5) for five pathotypes avirulent against *Yr4* and high ITs (7-9) for six pathotypes virulent against *Yr4* led to a postulation of *Yr4* in the tested genotypes in this resistance group (Tables 2 and 4). The IT profile of Hybrid 46 matched that of the tested lines except for the line with an intermediate IT of 5.

Two elite lines had resistance profiles similar to that of the Avocet *Yr6* tester line in tests against the 11 pathotypes (resistance group 7). Based on the high and low infection type patterns of the tested genotypes with the tester line Avocet *Yr6*, the tested genotypes were postulated to carry *Yr6* (Table 2). Five of the ICARDA elite bread wheat lines had high (7–8) and low (1–3) infection type patterns, similar to those of the tester variety Heines Peko when tested against the 11 pathotypes. Heines Peko is known to carry *Yr6* plus additional uncharacterized *Yr*-gene/s (Calonnec *et al*., 1997). These five elite lines (lines 2, 5, 47, 63, and 64), designated *Yr6+* in Table 2, were, therefore, also postulated to carry *Yr6* plus unknown additional gene/s.

Resistance group 8 included one Lebanese bread wheat variety with high ITs (8 to 9) for the pathotypes virulent against *Yr7* and low ITs (2 to 3) for the pathotypes avirulent against *Yr7*. The same infection type pattern was observed when the tester line Avocet *Yr7* was tested against the 11 *Pst* pathotypes (Table 3). Riechersberg 42 is known to carry *Yr7* and additional uncharacterized resistance genes (McIntosh *et al*., 1995). Based on the similarity of the infections patterns of Riechersberg 42, we postulated that *Yr7* and additional uncharacterized genes were present in the 15 elite lines and three Lebanese bread wheat varieties (Table 2).

The genotypes in resistance group 9 were postulated to carry *Yr9*. This group included four bread wheat elite lines. The postulation of *Yr9* in this group was based on similar infection type patterns for the tested lines Avocet *Y9* and Clement, in tests against the seven *Pst* pathotypes virulent against *Yr9*, and the four pathotypes avirulent against this gene (Tables 2 and 3).

Resistance group 10 included three elite lines postulated to carry *Yr17*. These lines had high ITs (IT = 8) against four pathotypes virulent against *Yr17*, and low ITs (2 to 3) for seven pathotypes avirulent against *Yr17*. These lines had resistance profiles similar to that of the tester line VPM1 (Table 2).

Resistance group 11 included one elite line, one Lebanese bread wheat variety (Florence Aurore) and two Lebanese bread wheat landraces (two accessions of Salamouni) which were postulated to carry *Yr25*, with low ITs (IT = 1) for the *Pst* pathotype avirulent against *Yr25*, and high ITs (7 to 9) against the other ten pathotypes virulent against *Yr25*. The resistance profiles of the genotypes postulated to carry *Yr25* were similar to that of the tester line TP981 used as source of *Yr25* in this study (Tables 2, 3 and 4).

Resistance group 12 included eight elite lines (Table 2) and five Lebanese bread wheat varieties (Table 3) postulated to carry *Yr27*. The tested genotypes had high ITs (7 to 8) for the only pathotype virulent against *Yr27*, and low ITs (1 to 5) for the remaining ten pathotypes avirulent against *Yr27*. These postulated lines had resistance profiles similar to that of the tester genotypes Avocet *Yr27* and Opata.

Resistance group 13 included the genotypes for which two *Yr* genes were postulated. Similarities in the infection type patterns of two tester genotypes tested against the 11 pathotypes (Table 1) and those of tested

elite lines, Lebanese varieties and landraces, were used to postulate gene combinations in the tested genotypes in this resistance group. In this group, combinations of *Yr6* and *Yr9* were postulated in only two ICARDA elite lines, *Yr6* and *Yr17* were postulated in three of these ICARDA lines, *Yr7* and *Yr1* were postulated in one ICARDA line, *Yr7* and *Yr4* were postulated in three ICARDA lines, *Yr9* and *Yr1*, were postulated in one ICARDA line, *Yr9* and *Yr3* were postulated one ICARDA line, and *Yr9* and *Yr4* were postulated in only four ICARDA elite lines (Table 2). Similarly, the combination of *Yr6* and *Yr7* was postulated in two Lebanese varieties, and the combination of *Yr6* and *Yr17* was postulated in one Lebanese variety (Table 3). With the 11 pathotypes used here, we were able to postulate all the *Yr* genes considered, except for *Yr32,* in the genotypes tested.

Evaluation of adult plant resistance

We evaluated the adult-plant responses of the tested genotypes by performing a field test with 44 ICARDA elite lines at two sites, one in Syria (Tal Hadya) and the other in Lebanon (Terbol). Table 5 shows the seedling and adult plant responses of the tested lines at the two sites, together with the postulated *Yr* genes. Genotypes were considered to carry only adult-plant resistance when the same genotype was susceptible (high ITs of 7 to 9) to pathotype 6E16*v9v27* at the seeding stage, but resistant at the adult-plant stage. Twenty nine out of 44 elites lines that were resistant at the seedling stage, showed low to moderate resistance at adult-plant stage. The elite lines 7, 12, 22, 29, 35, 51, 66, 67, 75, 85 and 87 (Table 5; Figure 2), which were susceptible at the seedling stage, were resistant at adult-plant stage. Elite line 70, which was resistant to the 11 pathotypes used in the gene postulation study, including pathotype 6E16*v9v27,* was also resistant in field tests.

Elite lines postulated to carry *Yr1* (lines 60, 61, and 65), *Yr3* (line 46), and *Yr4* (line 18) were resistant at both the seedling and adult-plant stages. The elite lines postulated to carry *Yr6* (lines 47, 63) and *Yr6*+ (64) were resistant in the field. The pathotypes used for inoculation in the field carried virulence against both *Yr6* and *Yr6*+. The field resistance responses of these lines can therefore be considered to indicate the presence of adult-plant resistance in these lines.

Eight lines carrying *Yr7* and additional uncharacterized seedling resistance genes (lines 25, 34, 36, 37, 41, 42, 44, and 68, Table 5) were resistant at both the seedling and adult-plant stages. The source of *Yr7* was susceptible at both the seedling and adult-plant stages and the *Yr7*+ source displayed intermediate field responses at the two sites. We therefore considered the strong field responses of the lines postulated to carry *Yr7*+ to be due to the combination of an uncharacterized seedling resistance gene and adult-plant resistance genes effective against the field pathotype at both sites.

The line postulated to carry *Yr17* (line 31) displayed an intermediate resistance response in field conditions. The seedling and field responses of the source of *Yr17* showed *Yr17* to be effective against the pathotype used for seedling and adult-plant assessment. Line 39 therefore probably carries *Yr17.* Three lines were postulated to carry *Yr27* (lines 1, 8 and 46), one of which, line 46, displayed moderate resistance at the adult-plant stage suggestive of the presence of adult-plant resistance genes in this line.

Line 51 displayed an adult-plant response of 5R in field conditions, but seedlings of this line had a high infection type with the pathotypes used. As the pathotypes tested were virulent against combinations of the *Yr6* and *Yr9* genes, the adult-plant resistance response of this line was considered to indicate the presence of adult-plant resistance in this line.

The *Yr6*+*Yr17* combination conferred resistance at both the seedling and adult-plant stages in the Lebanese field for lines 27 and 86, demonstrating the efficacy of *Yr17,* as virulence against *Yr6* was common in both the seedling and adult-plant tests. The line postulated to carry both *Yr7* and *Yr4* (line 4) was resistant at both the seedling and adult-plant stages, demonstrating the efficacy of *Yr4* in field tests. As *Yr1, Yr3*, and *Yr4* were effective against the pathotypes used in both seedling and adult-plant tests, the resistance response of combinations of *Yr9* with *Yr1* (line 84), *Yr3* (line 83), and *Yr4* (line 9) was due to the efficacy of *Yr1*, *Yr3*, and *Yr4* against the pathotypes used in the seedling and adult-plant tests.

Three of the tested lines for which the seedling resistance could not be postulated by multipathotype testing (lines 7, 22, and 85) were postulated to carry adult-plant resistance, given the high level of infection observed at the seedling stage.

Resistance diversity in Lebanese landraces

The landraces generally displayed considerable diversity in their response to the 11 pathotypes (Table 6; Figure S1). Many landraces displayed variation in their resistance responses to each pathotype, with 0 to 50% susceptible plants in resistant landraces and 0 to 50% resistant plants in susceptible landraces, for any given pathotype. The number of resistant plants was highest with the 6E16, 43E138 and 237E173*v17 (Oakley/ Solstice)* pathotypes, and lowest with 239E175*v17 (War-*

Table 5. Pedigree, postulated seedling-stage stripe rust resistance genes and field responses to stripe rust of 44 advanced bread wheat lines from ICARDA at the Tel Hadya (Syria) and Terbol (Lebanon) research stations.

Entry	Pedigree	Postulated *Yr* genes	Seedling infection type[a]	Adult-plant resistance[b]
11	Tracha'S'//CMH76-252/PVN'S'	Resistant[c]	2	20-30MR
20	Achtar*3//Kanz/KS85-8-4/3/Zemamra-5	Resistant	2	10MR
32	Blass-1/4/CHAT'S'//KVZ/CGN/3/BAU'S'	Resistant	1	50RMR
70	Crow'S'/Bow'S' -1994/95//Asfoor-5	Resistant	5	10R
12	W3918A/JUP	Susceptible[d]	7	10R
75	Nesma*2/14-2//2*Safi-3	Susceptible	8	5R
60	Crow'S'/Bow'S' -3-1994/95//Tevee'S'/Tadinia	*Yr1*	1	10MR
61	Tevee'S'/3/T.aestivum/SPRW'S'//CA8055/4/Pastor-2/5/Sunbri	*Yr1*	1	10MR
65	Qafzah-2/Ferroug-2	*Yr1*	2	10MR
46	Bow #1/Fengkang15/3/HYS//DRC*2/7C	*Yr3*	3	10R
18	SHA3/Seri//Yang87-142/3/2*Towpe	*Yr4*	2	20MR
67	Hamam-4/Angi-2	*Yr6*	8	10R
87	Hubara-16/2*Somama-3	*Yr6*	8	30R
47	MON'S'/ALD'S'//Towpe'S'	*Yr6*	5	10R
63	Weebill-1/2*Qafzah-21	*Yr6*	6	10RMR
64	Rebwah-12/Zemamra-8	*Yr6* +[f]	1	1R
34	Kauz//Kauz/Star	*Yr7* +	1	10MR
36	Cham-4/Shuha'S'/6/2*Saker/5/RBS/Anza/3/KVZ/HYS//YMH/TOB/4/Bow'S'	*Yr7*+	1	5R
37	Cham-4/Shuha'S'/6/2*Saker/5/RBS/Anza/3/KVZ/HYS//YMH/TOB/4/Bow'S'	*Yr7*+	1	5R
41	Florkwa-2/Asfoor-5	*Yr7*+	2	30MR
42	Ferroug-2/Potam*2KS811261-8//Zemamra-8	*Yr7*+	2	10R
44	Hubara-15/Zemamra-8	*Yr7*+	1	10R
19	Cham-4/Shuha'S'/6/2*Saker/5/RBS/Anza/3/KVZ/HYS//YMH/TOB/4/Bow'S'	*Yr7*+	1	5R
68	Shuha-5/Asfoor-1	*Yr7*+	1	10R
66	MON'S'/ALD'S'//Aldan'S'/IAS58/3/Safi-1/4/Zemamra-1	*Yr9*	8	10MR
29	Clement/ALD'S'//Zarzour/5/AU//KAL/BB/3/BON/4/KVZ//CNO/PJ62 (Sandall 3)	*Yr9*	8	5R
35	ICARDA-SRRL-5	*Yr9*	8	20R
31	Shuha-8//Vee'S'/Saker'S'	*Yr17*	2	40MRMS
1	Kauz = JUP/BJY//URES	*Yr27*	8	100S
8	Inqualab 91/Flag-2	*Yr27*	8	10S
10	Bow#1/Fengkang15/3/HYS//DRC*2/7C	*Yr27*	8	30MRMS
51	GV/ALD'S'/5/ALD'S'/4/BB/G11//CNO67/7C/3/KVZ/TI/6/2*Towpe	*Yr6* + *Yr9*	7	5R
27	DVERD-2/*Aegilops squarrosa* (214)//2*ESDA/3/NS732/HER	*Yr6* + *Yr17*	3	5R
86	Hubara-3/Angi-2//Somama-3	*Yr6* + *Yr17*	1	20R
4	Samar-8/Kauz'S'//Cham-4/Shuha'S'	*Yr7* + *Yr4*	2	5R
84	ACSAD 529/Karawan'S'//Somama-3	*Yr9* + *Yr1*	1	5R
83	Hubara-5/3/SHA3/Seri//SHA4/Lira	*Yr9* + *Yr3*	2	5R
9	Qafzah-33/Florkwa-2	*Yr9* + *Yr4*	4	5R
7	*T. aestivum*/SPRW'S'//CA8055/3/Bacanora86	Ni[e]	7	1R
22	Fow-2/SD8036//SafiI-3/3/NS732/HER//Kauz'S'	Ni	8	20MR
38	NS732/HER//Arrihane/3/PGO/Seri//BAU	Ni	8	40S
39	IZAZ-2//Tevee'S'/Shuha'S'	Ni	2	20R
54	Sakha73/5/IAS 58/4/KAL/BB//CJ'S'/3/ALD'S'/6/Goumria-12	Ni	2	20R
85	Girwill-13/2*Pastor-2	Ni	8	10R

[a] Infection type with 6E16*v*9v27, the predominant pathotype in the CWANA region for the 2010-2011 season, carrying the *v*2, 6, 7, 8, 9, 25, 27, and SD, based on pathotype surveys conducted by ICARDA for the same year.

[b] R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible, according to the modified Cobb scale of Peterson *et al*. (1948). The numbers 5-100 are the percentages of the leaf area covered by stripe rust. The score reported is the mean for two seasons in Syria, and three seasons in Lebanon.

[c] Resistant to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.

[d] Susceptible to all *Puccinia striiformis* f. sp. *tritici* pathotypes used.

[e] Ni indicates non-identified resistance genes.

[f] Additional and uncharacterized *Yr* genes.

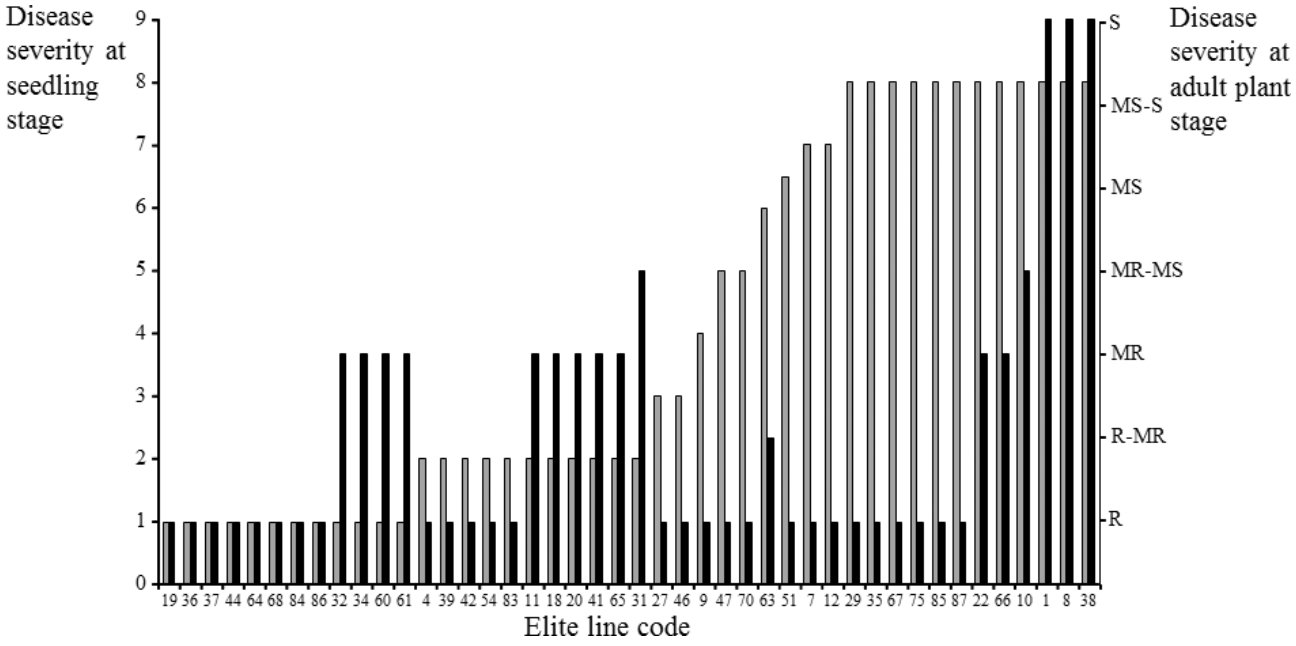

Figure 2. Disease severity at the seedling (gray columns) and adult-plant (black columns) growth stages, for 44 ICARDA bread wheat elite lines inoculated with the predominant pathotype for the 2010-2011 season in Lebanon and Syria. This pathotype carries *v2*, *6*, *7*, *8*, *9*, *25*, *27*, and *SD*, according to the pathotype surveys conducted by ICARDA for the same year. Disease severity at the seedling stage is scored from 0 to 9, where 0 was considered fully resistant and 9 fully susceptible (McNeal *et al.* 1971). At the adult-plant stage, disease severity was recorded as described by Roelfs *et al.* (1992); R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible. The codes of the elite lines are given in Table 5.

rior), which has the largest number of virulence factors. Interestingly, two durum wheat Bekaii landraces (landraces 24 and 27) from two different sites had 100% and 11% resistant plants, respectively, when tested with the pathotype 239E175*v17 (Warrior)*. These landraces thus carry new resistance genes that could not be detected with the pathotype arrays used here, but the uncharacterized genes in the resistant plants contributed to the resistance of the landraces, particularly in tests against the most virulent race, 239E175*v17 (Warrior)*.

PCA with 11 variables, including the percentage of plants differing from the most frequent reaction with each of the 11 pathotypes, separated the landraces in terms of their heterogeneity of reaction to all 11 pathotypes (Figure 3, Table 7). The two first axes accounted for 54.3% of the variance, with the most heterogeneous landraces to the right of axis 1 (landraces 27, 21, 24, 5, 2, 4, 23) and the most homogeneous ones to the left (landraces 10, 17, 18, 11, 15). Four of the seven most heterogeneous landraces were durum wheat landraces. Axis 2 separated landraces in terms of their heterogeneity of reaction to four pathotypes (three carrying *v7*: 6E16, 43E138, and 106E139). PCA with 11 variables, including the percentage of plants resistant to each of the 11 pathotypes, separated the landraces in terms of their level of resistance for their reaction to all 11 pathotypes (Figure 4; Table 8). The two first axes accounted for 70.1% of total variance, with the most resistant landraces to the right of axis 1 of the PCA (landraces 28, 24, 19, 27) and the most susceptible landraces to the left (landraces 10, 15, 17, 25). Five of the nine most resistant landraces were durum wheat landraces. Axis 2 separated landraces in terms of their resistance to four pathotypes (6E16, 6E16*v9v27*, 45E140 and 169E136*v17*).

DISCUSSION

Host resistance-based approaches remain the most economical and environmentally friendly method of controlling wheat rust diseases. Most of the characterized resistance genes are race-specific and conform to the well-described gene-for-gene model (Flor, 1956). A knowledge of the genetic structure of breeding lines and genetic resources is crucial for the breeding of more durable resistant genotypes and the efficient use of genetic resources. We postulated the *Yr* genes in 138 wheat genotypes from ICARDA, Lebanese varieties and landraces, using an array of 11 *Pst* pathotypes at the seedling stage. Using this set of pathotypes with

Table 6. Assessment of resistance heterogeneity in the wheat landraces, expressed as the percentage of resistant plants (R) among the susceptible landraces, and the percentage of susceptible plants (S) among the resistant landraces, for each of the 11 *Puccinia striiformis* f. sp. *tritici* pathotypes.

Landrace name	Location	Landrace Code	Species[b]	Pathotype[a]																					
				A		B		C		D		E		F		G		H		I		J		K	
				R[c]	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S
Salamouni[d]	Qamouaa, Akkar	1	TA	33[e]	-[f]	0	-	25	-	14	-	8	-	0	-	8	-	4	-	4	-	13	-	0	-
Salamouni	Fneidik, Akkar	2	TA	-	48	17	-	26	-	8	-	17	-	13	-	26	-	0	-	29	-	30	-	0	-
Salamouni	Qamouaa, Akkar	3	TA	0	-	28	-	19	-	-	46	0	-	0	-	0	-	0	-	19	-	26	-	0	-
Salamouni	Laklouk, Jbeil	4	TA	8	-	9	-	19	-	-	41	0	-	29	-	0	-	17	-	-	42	-	36	0	-
Salamouni	Laklouk, Jbeil	5	TA	50	50	32	-	13	-	7	-	9	-	36	-	0	-	0	-	32	-	50	50	0	-
Ukranian Variety	Tel Akhdar, Bekaa	6	TA	-	46	0	-	5	-	3	-	0	-	9	-	0	-	50	-	0	-	0	-	0	-
Ukranian Variety	Tel Akhdar, Bekaa	7	TA	41	-	13	-	16	-	0	-	12	-	18	-	0	-	38	-	4	-	0	-	0	-
Salamouni	Jeb Janine, Bekaa	8	TA	13	-	0	-	-	28	0	-	0	-	0	-	0	-	0	-	32	-	35	-	0	-
Salamouni	Jeb Janine, Bekaa	9	TA	0	-	11	-	22	-	0	-	4	-	16	-	0	-	11	-	48	-	20	-	0	-
Salamouni	Aarida, Akkar	10	TA	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-
Salamouni	Northern Bekaa	11	TA	0	-	0	-	-	0	0	-	4	-	5	-	0	-	0	-	0	-	0	-	0	-
Salamouni	Nabha, Bekaa	12	TA	50	50	0	-	40	-	8	-	4	-	10	-	0	-	0	-	0	-	0	-	0	-
Salamouni	Nabha, Bekaa	13	TA	-	0	0	-	4	-	4	-	4	-	0	-	0	-	4	-	4	-	4	-	0	-
Salamouni	Ham, Bekaa	14	TA	7	-	0	-	7	-	0	-	0	-	7	-	4	-	0	-	4	-	4	-	0	-
Salamouni	Ham, Bekaa	15	TA	7	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-
Salamouni	Aarsal, Bekaa	16	TA	0	-	0	-	4	-	0	-	23	-	0	-	4	-	0	-	0	-	0	-	0	-
Salamouni	Northern Bekaa	17	TA	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-
Salamouni	Northern Bekaa	18	TA	-	0	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-
Nessr	Tal Amara, Bekaa	19	TA	-	0	-	0	-	25	-	0	8	-	-	0	0	-	0	-	0	-	0	-	0	-
Awnless Variety	Qamouaa, Akkar	20	TA	-	0	-	0	19	-	10	-	0	-	0	-	9	-	4	-	5	-	4	-	0	-
Abou Shwereb	Qamouaa, Akkar	21	TD	26	-	-	26	34	-	19	-	16	-	13	-	23	-	9	-	30	-	50	50	0	-
Abou Shwereb	Qamouaa, Akkar	22	TD	0	-	0	-	15	-	0	-	8	-	10	-	8	-	4	-	9	-	8	-	0	-
Abou Shwereb	Fneidik, Akkar	23	TD	-	0	-	42	0	-	0	-	0	-	47	-	0	-	0	-	43	-	36	-	0	-
Bekaii	Jeb Janine, Bekaa	24	TD	19	-	38	-	-	31	35	-	4	-	37	-	12	-	50	-	-	0	-	20	-	0
Abou Shwereb	Aarida, Akkar	25	TD	5	-	8	-	0	-	0	-	4	-	0	-	0	-	0	-	0	-	0	-	0	-
Haurani	Tal Amara, Bekaa	26	TD	0	-	-	4	17	-	0	-	0	-	0	-	0	-	0	-	0	-	22	-	0	-
Bekaii	Tal Amara, Bekaa	27	TD	-	33	-	13	-	26	-	43	4	-	36	-	0	-	12	-	-	39	39	-	11	-
Waha	Jeb Janine, Bekaa	28	TD	-	13	-	8	-	0	-	0	-	0	-	8	-	0	-	0	-	0	-	0	-	0

[a]A = 6E16, B = 6E16*v9v27*, C = 43E138, D = 45E140, E = 106E139, F = 169E136*v17*, G = 232E137, H = 237E141, I = 237E141*v17*, J = 237E173*v17 (Oakley/Solstice)*, K = 239E175*v17 (Warrior)*. Pathotypes are coded according to Johnson *et al.* (1972).
The virulences and avirulences tested were 1, 2, 3, 4, 6, 7, 8, 9, 17, 25, 27, 32, SD, SP, Su.
[b] TA = *Triticum aestivum* (L), TD = *T. durum*.
[c] R = seedling resistant (low infection type of 0-6), S = seedling susceptible (high infection type of 7-9).
[d] 30 seedlings per landrace and per pathotype were tested.
[e] Percentage of resistant (R) plants in a mainly susceptible landrace and percentage of susceptible (S) plants in a mainly resistant landrace.
[f] indicates missing data.

complementary virulence spectra, we were able to infer the resistance profiles of most of the lines tested. The 11 pathotypes used here discriminated between the *Yr1*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr17*, *Yr25*, *Yr27*, *Yr32*, *YrSD*, *YrSu* and *YrSP* genes, and we were able to postulate *Yr1*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr9*, *Yr17*, *Yr25* and *Yr27* singly or in combination in the tested genotypes. These results highlight the utility of this pathotype array for the detection of *Yr* genes. However, a group of genotypes (Group 3) remained for which seedling resistance could not be explained with the pathotypes, and for which the resistance genes present remained unknown. Based on the resistance responses of these genotypes to the wide array of virulence factors of the 11 pathotypes, we postulated that these genotypes might be sources of new stripe rust resistance genes.

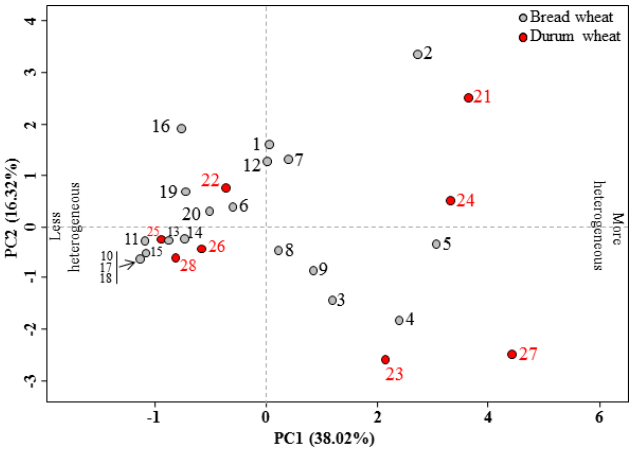

Figure 3. Plot of the first (PC1) and second (PC2) principal component means from an analysis of the 11 variables (percentage of resistant plants in susceptible landraces and percentage of susceptible plants in resistant landraces, for each of the 11 *Puccinia striiformis* f. sp. *tritici* pathotypes, for 28 Lebanese landraces (1-28)), as described in Table 7. Gray symbols = bread wheat, red symbols = durum wheat.

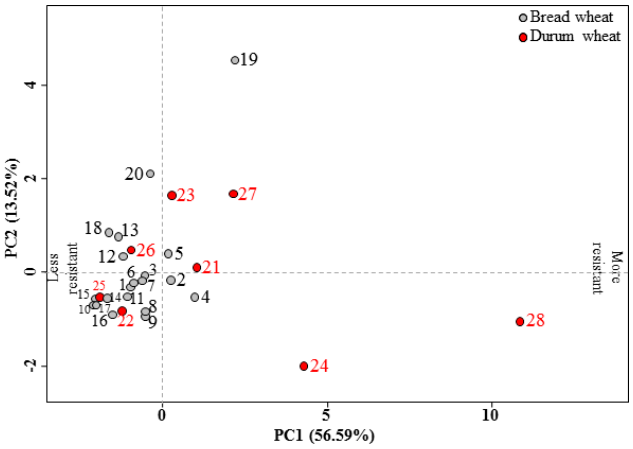

Figure 4. Plot of the first (PC1) and second (PC2) principal component means from an analysis of the 11 variables (percentage of plants resistant to each of the 11 *Puccinia striiformis* f. sp. *tritici* pathotypes, for 28 Lebanese landraces (1-28)), as described in Table 7. Gray symbols = bread wheat, red symbols = durum wheat.

In resistance group 1, 9% of ICARDA elite lines and 9% of Lebanese varieties displayed complete resistance to all pathotypes. Among the resistant Lebanese varieties, only two durum wheat genotypes displayed full resistance. None of the Lebanese bread wheat varieties were completely resistant to all pathotypes. Only one durum wheat landrace was completely resistant to all pathotypes.

With the exception of a few uncharacterized elite lines and landraces, the ICARDA elite lines and Lebanese varieties generally carried at least one effective *Yr* gene providing resistance to at least one of the 11 *Pst* pathotypes, whereas 75% of landraces were susceptible to all

Table 7. Eigen vectors of the two principal components axes (PC1 and 2) for the 11 variables assessed (resistance heterogeneity in the landraces expressed as the percentage of resistant plants in susceptible landraces and the percentage of susceptible plants in resistant landraces, for each of the 11 *Puccinia striiformis* f. sp. *tritici* pathotypes), and their contributions to the variance.

Variables[a]	PC1	PC2
A	0.53	0.42
B	0.76	-0.15
C	0.63	0.37
D	0.67	-0.23
E	0.28	0.75
F	0.80	-0.30
G	0.43	0.71
H	0.33	0.10
I	0.74	-0.31
J	0.86	-0.15
K	0.42	-0.36
Eigen value	4.18	1.80
Percentage of variance (%)	38.02	16.32

[a]A = 6E16, B = 6E16*v9v27*, C = 43E138, D = 45E140, E = 106E139, F = 169E136*v17*, G = 232E137, H = 237E141, I = 237E141*v17*, J = 237E173*v17 (Oakley/Solstice)*, K =239E175*v17 (Warrior)*.

Table 8. Eigen vectors of the two principal components axes (PC1 and 2) for the 11 variables assessed (percentage of plants resistant to each of the 11 *Puccinia striiformis* f. sp. *tritici* pathotypes for Lebanese landraces), and their contributions to the variance.

Variables[a]	PC1	PC2
A	0.53	0.42
B	0.76	-0.15
C	0.63	0.37
D	0.67	-0.23
E	0.28	0.75
F	0.80	-0.30
G	0.43	0.71
H	0.33	0.10
I	0.74	-0.31
J	0.86	-0.15
K	0.42	-0.36
Eigen value	4.18	1.80
Percentage of variance (%)	38.02	16.32

[a]A = 6E16, B = 6E16*v9v27*, C = 43E138, D = 45E140, E = 106E139, F = 169E136*v17*, G = 232E137, H = 237E141, I = 237E141*v17*, J = 237E173*v17 (Oakley/Solstice)*, K = 239E175*v17 (Warrior)*.

pathotypes. Nine of the resistance genes tested (*Yr1*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr9*, *Yr17*, *Yr25* and *Yr27*) were postulated singly in ICARDA elite lines; *Yr7*, *Yr9*, *Yr25* and *Yr27* were detected in Lebanese varieties and only *Yr3*, *Yr4* and *Yr25* were detected in some landraces. *Yr27* was the most frequent *Yr* gene postulated singly in the Lebanese varieties. *Yr7* in combination with other unidentified *Yr* genes was postulated with the highest frequency in ICARDA elite lines. Combinations of two *Yr* genes were found in 16% of ICARDA elite lines: *Yr6+Yr9*, *Yr6+Yr17*, *Yr7+Yr1*, *Yr7+Yr4*, *Yr9+Yr1*, *Yr9+Yr3*, and *Yr9+Yr4*. The *Yr6+Yr7* combination was found in two Lebanese varieties and *Yr6+Yr17* was found in one landrace only. Only one awnless landrace (BW) contained *Yr3*. Only one Lebanese bread wheat landrace (Nessr) had *Yr4* and two Salamouni bread wheat landraces had *Yr25*. The postulated *Yr* genes, either singly or in combination, were more frequent in Lebanese varieties than in landraces. ICARDA elite lines displayed greater diversity for the postulated *Yr* genes than the Lebanese varieties and landraces (Figure 1).

In general, our study revealed a narrow genetic basis of resistance in the genotypes tested for seedling resistance genes in the absence of effective adult-plant resistance genes, but we did not investigate or characterize such adult-plant resistance genes in this study. With the exception of *Yr3* and *Yr4,* and, to some extent, *Yr1,* which are effective in most of the wheat growing areas in CWANA, the rest of postulated genes were not effective against current pathotypes. The *Yr1*, *Yr3*, and *Yr4* genes will also cease to be effective if the North Western European pathotypes spread to the CWANA region. With the recent incursion of the Warrior pathotype into CWANA, the efficacy of these three *Yr* genes is dwindling, and their use in breeding for rust resistance cannot, therefore, be recommended unless they are used in combination with effective seedling resistance genes and/or adult-plant resistance genes.

Yr1 was postulated in only 6% of ICARDA elite lines. Despite the efficacy of *Yr1* in most of the wheat-growing areas of CWANA, virulence against *Yr1* has been reported in East Asia (Stubbs, 1985), Central Asia and the Caucasus region (Yahyaoui *et al.,* 2002) and Syria (K. Nazari unpublished data), highlighting the race specificity of this gene. Considering the specificity of *Yr1* and the presence of pathotypes virulent against this gene in the *Yr27*-virulent group (Mogens Hovmoller, personal communication), together with the recent spread of the Warrior pathotype to North Africa, Turkey, and Azerbaijan from Europe, the use of elite lines and commercial cultivars bearing only *Yr1* should be restricted in CWANA.

Yr3 and *Yr4* were infrequent in the lines tested. These two resistance genes are very common in winter wheat cultivars and breeding lines in North Western Europe (de Vallavieille-Pope *et al*., 1990; 2012). However, despite the low frequency of virulence against these two genes in most of the wheat-growing areas of CWANA, sources of *Yr3* and *Yr4* have not been widely used in breeding for stripe rust resistance in spring wheat genotypes. Virulence against these two genes is very common within the *Pst* population in Europe and Australia (de Vallavieille-Pope *et al*., 2012; Wellings, 2011). *Yr3* and *Yr4* can no longer be recommended as sources of resistance in CWANA, due to the recent spread of the Warrior race to some of the wheat-growing areas of North Africa and West Asia.

Yr6 was postulated singly or in combination with *Yr9* or *Yr17* in 13% of ICARDA elite lines and in combination with *Yr7* in 9% of Lebanese varieties. Varieties carrying *Yr6* were introduced into the CIMMYT wheat breeding program and, hence, into ICARDA germplasm, as sources of leaf rust resistance, including *Lr13* and *Lr34* (Wellings, 1986). However, *Yr6* was not frequent in the ICARDA lines tested and virulence against *Yr6* has been reported to be fixed in all isolates from Asia, Africa and South America tested (GRRC, 2017).

Yr7 was postulated singly in only one Lebanese bread wheat variety (Haramoun) and in combination with additional genes in other two Lebanese bread wheat varieties, Tannour and 885, and 15 elite lines. *Yr7* originated from the durum wheat cv. Iumillo. The gene was transferred to Thatcher wheat, from which the differential variety Lee was derived (McIntosh *et al*., 2012). *Yr7* is present in a range of winter and spring wheat cultivars (McIntosh *et al*., 2012). This gene has been defeated in the CWANA region and is no longer effective against the prevalent pathotypes in this region.

Yr9 was postulated singly in four ICARDA elite lines (5%) and in combination with *Yr1*, *Yr3* and *Yr4* in six elite lines (7%). This gene originated from *Secale cereale* and is linked to *Lr26* and *Sr31* in the 1BL.1RS translocation (McIntosh *et al*., 2012). During the 1990s, most of the adapted wheat germplasm generated and distributed by CIMMYT in spring wheat production areas at low latitudes carried the 1BL.1RS translocation (Bimb and Johnson, 1997). This translocation was also identified in European wheat germplasm by Mettin *et al*. (1973) and Zeller (1973). Virulence against *Yr9* has been common in wheat-growing areas in CWANA and sub-Saharan countries since the 1980s, particularly in countries in which 1B.1R-containing genotypes were distributed, including Ethiopia (Badebo and Bayu, 1992), Syria (Mamluk and El-Naimi, 1992), Turkey (Dusunceli *et al*., 1996), Iran (Torabi *et al*., 1995), Pakistan (Bahri *et al.,* 2011), and in Central Asia and Caucasian countries (Yahyaoui, 2005).

The use of this gene in breeding materials should therefore be restricted.

Yr17 was postulated singly in three ICARDA elite lines (3%) and in combination with *Yr6* in one Lebanese bread wheat variety (Naama). The *Yr17*, *Lr37* and *Sr38* gene cluster was transferred to wheat in a translocation from *Aegilops ventricosa* (Dousssinault *et al*., 1998). It was originally transferred to the VPM1 line (a cross of *Ae. ventricosa*, *Triticum persicum* and *cv.* Marne Desprez) (Bariana and McIntosh, 1993). Virulence against *Yr17* has been detected in the USA (Line *et al*., 1992), and in North Western Europe (Bayles *et al*., 2000; Hovmøller *et al*., 2002), where it remains frequent (de Vallavieille-Pope *et al*., 2012). The emergence of virulence against *Yr17* with the incursion of the Warrior race into North Africa (Hovmoller *et al*., 2016) and Turkey (Mert *et al*., 2016) should restrict the use of *Yr17* sources in isolation. Most of the French isolates studied here carry virulence against *Yr9* and *Yr17,* and it is therefore difficult to postulate these two genes when they are present singly. The use of diagnostic molecular markers for these genes can be very useful.

Yr25, which is common and ineffective in North Western European wheat varieties, was postulated in ICARDA elite line Nayzak-3 (line 15), one Lebanese variety (Florence Aurore), and two accessions of the Salamouni landrace. Virulence against *Yr25* is frequent in CWANA (Yahyaoui *et al*., 2002, Nazari, unpublished data).

Yr27 was postulated in five Lebanese varieties (22%) and eight ICARDA elite lines (9%). This gene originated from the wheat cultivar Selkirk and derivatives of the cultivar 'McMurachy' (Wellings, 1992), a parent of 'Selkirk'. This gene is also present in many CIMMYT genotypes (Wellings, 2011). Virulence against *Yr27* has been detected in New Zealand (Wellings and Burdon, 1992), Pakistan (Bahri *et al*., 2011; Ali *et al*., 2014), India (Prashar *et al*., 2007), Tajikistan, Kyrgyzstan (Singh *et al*., 2004), Iran (Nazari and Torabi, 2000) and Syria (Nazari *et al*., 2011). In the last few years, major wheat stripe rust epidemics have occurred in CWANA, sub-Saharan Africa, the Caucasus region and the Indian subcontinents, mostly due to the widespread cultivation of *Yr27* genotypes (Atilla and Kauz derivatives). Interestingly, that the Warrior pathotype does not carry virulence against *Yr27* and *Yr27* wheat cultivars may therefore once again come to predominate in the region.

In Lebanon and Syria, in 2010/2011, the *Yr1*, *Yr3* and *Yr4* genes remained effective, but virulence against *Yr2*, *Yr6*, *Yr7*, *Yr9*, *Yr25*, and *Yr27* predominated, with virulence against *Yr8* and *Yr17* occurring at only low to moderate frequencies (El Amil *et al*., in press).

Adult-plant resistance is often race non-specific and more durable than race-specific seedling resistance. Adult-plant resistance is generally controlled by temperature-sensitive, minor or additive genes. The presence of adult-plant resistance genes has been reported in various winter and spring wheats (Johnson, 1980; Singh and Rajaram, 1994; Chen *et al*., 2014).

We therefore tested adult-plant resistance in Lebanese and Syrian fields, for a subset of elite lines. The three lines with *Yr1* were moderately resistant in the field and virulence against this gene (*v*1) was not detected in the survey conducted in 2010-2011; *v*1 may therefore have been present, at low frequency, at Terbol (LB). Lines 63 and 64, which carry *Yr6,* were resistant and moderately resistant, respectively, in the field, despite the presence of *v6* in Syria and Lebanon, indicating the presence of additional adult-plant resistance in these lines. Line 34, which carries only *Yr7,* was less resistant in the field than line 4, which carries the *Yr7*+*Yr4* combination. Given that the *Yr4* elite line 18 tested was moderately resistant when tested at Terbol (LB), the *Yr7*+*Yr4* combination seems to be responsible for conferring full resistance. The combination of two seedling resistance genes, *Yr7*+*Yr4,* was effective at both sites. Line 1, in which *Yr27* was postulated singly, was susceptible in Syria. Elite line 8 was susceptible in Lebanon and line 10 was moderately resistant to moderately susceptible, suggesting that line 10 displayed adult-plant resistance. The adult-plant resistance test confirmed the presence of *v27* in Syria and Lebanon in 2010 and 2012.

Seedling resistance is of short duration and is rapidly overcome by the pathogen population in the absence of adult-plant resistance. Combinations of seedling resistances prolong the efficacy of the genes, but are rarely durable. Quantitative trait loci (QTLs) for adult-plant resistance provide partial resistance, but seldom protect the plant early in its life. A combination of both types of resistance is, therefore, crucial for the protection of the plant throughout the entire growing season. Durable stripe rust resistance has been observed in four French cultivars and one English cultivar combining both seedling resistance genes and QTLs active at the adult plant stage: *cv.* Renan (Dedryver *et al*., 2009), *cv.* Camp Rémy (Mallard *et al*., 2005), *cv.* Apache (Paillard *et al*., 2012), *cv.* Soissons (de Vallavieille-Pope *et al*., 2012) and *cv.* Claire (Powell *et al*., 2013).

Landraces are considered to be potential sources of disease resistance and agronomic traits. Considerable heterogeneity has already been reported, for plant height and days to heading, in Israeli bread and durum wheat landrace populations (Beharav *et al*., 1997), and has been advocated as a potential source of stripe and

leaf rust resistance in nine Chinese landraces (Zhang, 1995). Our study confirms that landraces are composed of several genotypes, and it will be of particular interest to investigate resistance genes in the genotypes resistant to 239E175*v17 (Warrior)*, the most frequent pathotype in North Western Europe. Further studies may determine whether the resistance gene found in the landraces differs from the genes already identified, and whether resistant landraces could be exploited for rust resistance and other agronomic traits.

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